A FURTHER ACCOUNT OF THE MURID, PSEUDOMYS (GYOMYS) APODEMOIDES FINLAYSON

By H. H. Finlayson

[Read 10 August 1944]

Plates XII to XV

This small native mouse, allied to the Western Australian *albocinereus*, was discovered by Mr. Walter Harvey in the upper South-Eastern district of South Australia in April 1929. Three years later further specimens having been obtained, the present writer published a preliminary description of the new species under the above name, in Trans. Roy. Soc. S. Aust., 1932, **56**, 170. Since then additional field work, observation of the animal in captivity, and the building up of a much more adequate series of preserved specimens have provided data for the following more extended account. This, while still incomplete in some respects, permits of detailed comparison with other species similarly treated and may lead to a juster estimate of its relation to its allies when these, in turn, are sufficiently known.

The writer records his appreciation of the co-operation of Mr. Harvey, in all matters attending the field work upon the animal, the results of which have been much enhanced by his ready and generous help.

Distribution and Habits

Practically the whole series obtained so far has come from a comparatively small area on Mr. Harvey's holding in the Hundred of Coombe, and the only extension of range which is definitely based upon specimens taken is at Pringatoola, 27 miles west-south-west of Coombe and within eight miles of the Coorong coast. Less definite but still reliable evidence, derived from the presence of its characteristic burrows and tracks and middens thereon, indicate its occurrence at several other points in the counties of Cardwell and Buckingham, both east and west of the railway. Combinations of topography, soils and vegetations quite similar to that of the type habitat at Coombe are to be found over a wide area in the Murray Mallee and South-Eastern Divisions of South Australia and adjacent tracts of other States, and it seems certain that it will eventually prove to have a wide distribution herein; so far, however, neither observation nor enquiry supported by the submission of specimens, have disclosed the animal beyond the above mentioned counties.

The type locality at Coombe lies just within the limits of the South-Eastern District, but in topography and general aspect is quite similar to much of the so-called Ninety Mile Desert, further north in Chandos and Buccleuch. The general relief is lower; the considerable east and west limestone ridges of the Upper Desert are absent and the sandridges with their characteristic serrate profiles are replaced by lower undulations or isolated hills. There is a fairly sharp partition of soils into reddish loams of moderately firm texture and pure white sand, with corresponding local differences in vegetation. The loamy flats are now frequently cultivated, but primitively support a sparse savannah of the so-called Desert Gum (*Eucalyptus fasciculosa*), which here tends to be considerably larger than further north and commonly attains to 30-40 feet in height, and in some favoured oases to considerably more; the floor is here open, sparsely grassed, but frequently carries abundant Triodia (*T. basedowei* and *T. irritans*). The white sand tracts

support a dry type heath with honeysuckles (*Banksia marginata* and dwarf *B. ornata*), bulloak (*Casuarina pusilla*), needle bush (*Hakea ulicina*), yacka (*Xanthorrhea australis*), white mallee (*Eucalyptus angulosa*) and broom (*Baeckea* spp.) as the chief of the taller shrubs, while in the undergrowth the more prominent species are, *Adenanthos terminalis, Brachyloma ericoides, Astroloma conostephioides, Daviesia brevifolia, Leucopogon woodsii, Correa rubra, Thomasia petalocalyx, Hibbertia* spp., *Calythrix* cf. *tetragona, Leptospermum myrsinoides, Kunzea pomifera* and *Lepidosperma laterale*.[1]

Dense, uniform mallee communities of large extent are not a characteristic feature, as they are further north. The annual rainfall of 20 inches is considerably higher than in the Desert, and the heath undergrowth tends to be denser and richer in species.

So far the new species has been taken only in the sandy heath country, where it lives in scattered isolated colonies, with much apparently suitable country unoccupied. Its mode of life is very unobtrusive; it is almost strictly nocturnal, does not invade houses nor camps nor cultivated ground, and even in the immediate vicinity of its living sites it is seldom sufficiently numerous to cause any appreciable disturbance in the vegetation in feeding, or to make obvious pads. The sand heaps at its burrows at certain times of the year are practically the only external evidence of its presence which can be seen, and these, except when newly thrown up, are usually quite inconspicuous. Nevertheless, in spite of this obscurity, it seems somewhat remarkable that in a district that has been settled and farmed for eighty years it should not have been noticed before; none of Mr. Harvey's neighbours had cognisance of it, and the results of enquiry elsewhere have always been negative.

It is satisfactory to be able to record (as a rare good deed of a rather sinister domestic figure) that the original specimen was brought in by a house cat. Attempts at trapping were shortly afterwards undertaken, but the species proved very difficult to take in this way, both with ordinary baits which are generally successful with local murids, and special foodstuffs, and lures such as rhodium and anise oils were unavailing. The next few specimens to be got were found accidentally trapped in empty post-holes, a fate which it sometimes shared with *Dromicia concinna*, which occupies the same heaths. This fortunate accident suggested the deliberate use of pitfalls as a method of capture. The venture was quite successful, and nearly all subsequent catches were got by this device. The method followed was to sink ordinary post-holes about nine inches square and three feet deep, at random in the heath; when a catch was made, the holes were multiplied until as many as twenty in an acre were in use. In this way, ten have been taken in a night, and in most cases the catch was found alive and quite uninjured. The captives usually accepted their fate, temporarily at any rate, with resignation, and sought additional shelter by excavating a cavity into the wall of the hole at the bottom, whence as many as five close-packed adults have been removed in the morning; a few, however, escaped from time to time by the feat of climbing the vertical friable walls, and still others by driving nearly vertical shafts from the shelter pocket to the surface.

There is a marked periodicity in the success of the pitfall; the holes have been left uncovered at all times of the year, but practically all catches have been concentrated into the period of autumn and early winter, and within this period again there is unmistakable evidence of heightened activity immediately before or during

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[1] I am indebted to Miss Constance Eardley, of the Botany Department of the University of Adelaide, for naming the collection of plants made at Coombe; a few species were indeterminate through absence of flowers or fruit, but the above list includes all which are quantitatively important in the habitat of *apodemoides*.

rains and at times of unsettled weather—a trait of the species strikingly confirmed later in captivity. During the summer months it virtually disappears at Coombe, but whether through some change of habits placing it beyond easy observation, or through a definite exodus to other areas, is still uncertain.

The animal is an expert burrower and makes elaborate and relatively large warrens in which, during the cold weather, the whole of the daylight hours are spent, and in which the young are born and reared. The chief external evidence of a burrow site is a heap of white sand thrown up behind a circular aperture of about one inch in diameter, both commonly at the base of a heath banksia. This entrance, however, is but a temporary one, opened in autumn for renovation of the interior, and it is soon afterwards closed from within by a long sand plug. The real entrances are at a considerable distance from this one and unlike it, are very inconspicuous and take the form of circular popholes communicating with nearly vertical shafts. The general topography and architecture of the warren is shown in the scale diagram (fig. 1) of a comparatively elaborate one excavated at Coombe in June 1933. The following itemized description will serve as a legend for this diagram:

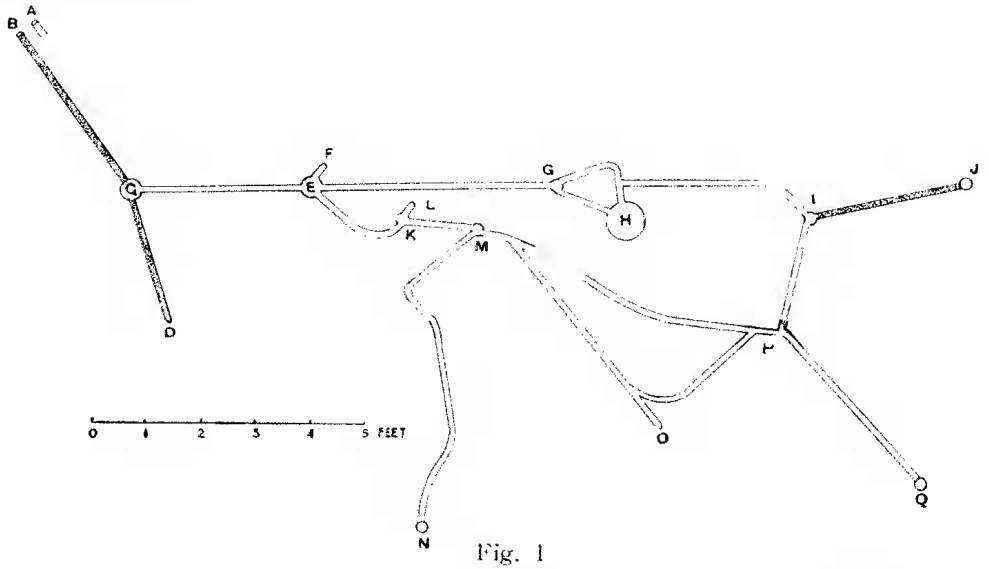

Fig. 1

A, trial opening, abandoned. B–C, the opening drive; horizontal diameter one inch, vertical diameter 1½ inches; descending evenly from ground level at B to 18 inches at C; this drive is now disused and functions as a dump, being loosely packed with sand from other parts of the galleries. C, a circular chamber, approximately three inches in diameter, such as commonly occurs elsewhere at major junctions. C–D, the first lateral drive descending to two feet at D, and sand plugged like B–C. C–E–G–I is the main longitudinal drive, maintaining a nearly constant direction except opposite the nest, where there is an acutely angled bypass; it descends to a maximum depth of about two feet six inches at the nest. E. G. I. K. M. are circular chambers of varying size, analogous to C. F, L, O are short drives used as dumps and loosely packed with sand. H is the nest chamber; it is a spherical cavity with a diameter of six inches and has two short independent tunnels connecting with the main drive, and can thus be completely by-passed by the ordinary traffic of the warren. The nest almost fills the sand cavity and is beautifully fashioned of finely shredded bark fibre, derived from a plant not yet identified, but apparently not occurring in the immediate vicinity of the burrow. In the centre of the mass is an inner cavity, smoothly lined with carefully adjusted

leaves of *Banksia marginata*, and when opened it was found to be occupied by four nestlings of about 10 days' growth. I–J is a continuation of the main drive which has been used as a sand dump in the same way as B–C; it rises slightly towards J, where it suddenly terminates in a nearly vertical shaft, leading directly to the surface two feet above; both vertical shaft and pophole are open, but of course isolated from the rest of the system and non-functioning. E–M–P–Q is the main lateral system and, with its branches, is similar to the main gallery, but over its middle course is from three to six inches deeper. The drives, P–Q and M–N, rise slightly towards their extremities, where they are converted abruptly into nearly vertical shafts, reaching the surface two feet six inches above the points Q and N, in the form of circular apertures of one-and-a-half inches diameter; these two popholes were the only functioning entrances and exits discovered, and presumably are used indifferently for both purposes.

Apart from the nest chamber, no other cavities suggesting living quarters were found, and, apart from the breeding nest, there was a complete absence of vegetable matter which might serve as fodder or bedding; the tunnels everywhere showed clean, smooth sandy floors free from excrement, and the nest was dry and non-odorous. Defaecation on the surface is sometimes concentrated upon middens, as mentioned above. The circular chambers at the junctions of passages are possibly made in the first place to facilitate the work of burrowing, and then left to facilitate traffic, though if this is so it is curious that this feature is not always present, even at three-way junctions. The combined lengths of all galleries in this warren, including the three vertical shafts, was approximately 60 feet, and the estimated weight of the moist sand displaced 40-50 pounds; a work of considerable magnitude for so small and delicate a creature. The volume of the sand in the dumps external to the warren was, unfortunately, not ascertained, but that it does not represent the whole volume displaced is clear from the obvious use made of unwanted passages, for the accommodation of part of it. The plug of replaced sand was always found to have a looser texture than the virgin consolidated soil, and a slightly different colour also, so that there was little difficulty in following the course of these packed tunnels by visual inspection during the digging.

Each excavation appears to be originally the work of one breeding pair, but the part-grown young of one or more litters may share the shelter with the parents. Seven individuals is the maximum number taken so far from one system. When young examples taken in a pitfall are released near a burrow, they will not enter unless they are satisfied that it is their own domicile. Uncertainty still prevails as to the duration of occupation of the burrow. Excavation of new holes and renovation of old ones is first noticed in early autumn, when the dumps of recently turned white sand at the entrance hole are, for a time, rather conspicuous. As this time also marks the beginning of the chief reproductive period, there seems no doubt that the two activities are correlated, and that the excavation is made primarily as a shelter for the young. Investigation of the warrens in summer is not sufficiently complete to prove that a general vacation of the same takes place, but there is much evidence in support of this, and at Coombe, the only examples taken on the surface in daylight have been in midsumer. At the Coorong site of Pringatoola, where it was trapped in late November, there was no evidence of burrowing, though it was so plentiful as to form noticeable pads in some favoured spots, with well-used circular middens; features never seen at Coombe.

Observations on the animal in captivity show that it is rather intolerant of heat and, as the local summer is a severe one, it is difficult to see why it should forsake the coolness of its underworld for the discomfort of the surface. It is possible, of course, that the move is involuntary and forced upon it by changes in

the texture of the drying sand; similar considerations have been shown to operate powerfully on the burrowing habits of some old world Muridae.

The natural enemies of the species at Coombe are probably chiefly predatory night birds. Burrows partly dug out by foxes have, however, been observed, and Mr. Harvey on one occasion found a small brown snake (*Demansia textilis*) within, and on another a spotted Pardalote (*Pardalotus punctatus*). Neither this snake, taken *in situ*, nor others taken at random in the district, contained *apodemoides* in the stomach, though they did contain house mice.

In general aspect the mouse is exceedingly delicate and attractive and remarkable for the prevailing pallor, not only of its pelage but of all exposed epidermal areas as well, which are nearly destitute of pigment and appear bright pink in life. In size and bulk, *apodemoides* is somewhat larger than an average house mouse, but is very dissimilar in general appearance and mannerisms. The build is rather squat as to body but with light slender appendages; the squatness is especially characteristic of some subadult phases, but in all is exaggerated, as is also the apparently large size of the head, by the erect and profuse pelage.

Observed in captivity, its slow movements and some of its postures are by no means graceful; when deliberately investigating its surroundings in a new cage, it has a curious pottering uncertain gait and the long slender tail is carried in a rather odd way, well clear of the ground and sometimes arched over the back. When startled, however, or otherwise excited, it is capable of movements of lightning-like rapidity and great precision—in both respects recalling *Notomys*. As noted above, examples on more than one occasion made their escape from vertical three-foot holes by climbing the sides, but in captivity it shows little inclination or aptitude for climbing. Much of its time, when stationery, is spent reared up on its haunches, when it assumes a comical, almost globular shape; its feeding is usually done so, and, if of suitable size, each particle such as a grain of seed or a berry, is taken delicately in the two hands and brought up to the mouth for the incisors to work upon, which they do with the utmost precision and speed and control, rejecting in the case of a wheat grain the whole of the husk, so that the cages soon become carpeted with discs of bran. Its feeding, indeed all its activities, are interrupted abruptly and frequently, for the toilet of the coat, which it keeps in immaculate condition; the toilet is done largely by the manus and incisors, the mysticial vibrissae receiving especially frequent attention.

In temperament it is both brisk and adaptable, docile and confident. Its nonchalance in the pitfall has already been mentioned; when removed by hand it showed little resentment and made no serious attempt to bite. When transferred to box cages and compelled to live in radically strange surroundings and upon a totally new and unaccustomed diet, it retained a cheerful activity with every evidence of comfort and content.

The cages used for parties of from five to ten were airy boxes three feet by three feet by two feet, with two glass sides and two of wire gauze to facilitate observation and ventilation and cooling, respectively. Shelter and nesting boxes with light hinged lids, and packed with wood-wool and cotton for nesting material, were provided, and were at once approved and adopted by the mice, but their sense of security evidently demanded emergency exits, which they promptly supplied by driving popholes through the deal walls. The cages were kept under a roofed shelter in a comparatively subdued light, and under these conditions they frequently left the nest during daylight for short tours of the cage, but all their main activity remained definitely crepuscular and nocturnal and involved an immense amount of coming and going, as the quantity of sand shifted plainly showed. The floor of the cages was covered with a layer of sand two inches deep,

and it was early discovered that a moist atmosphere was greatly appreciated. On several occasions when the sand dried out it was hosed lightly to remoisten it, and the effect on the colony was electrical; the mice left the shelter box *en masse*, though it was broad daylight, and engaged in a most animated display of acrobatics. The chief evolution was a lightning-like looping of the loop, by springing from the floor to a wall, thence to the roof, thence to the opposite wall and down to the floor, each impact, though of scarcely perceptible duration, being sufficient for attaining a new impetus; the looping was repeated a dozen times or more in a continuous series without pause.

They quarrelled very little among themselves, and a dozen might safely be left to share the same quarters; such bickering as did go on was of a mild kind and usually resulted in nothing more serious than tail shortening. One or two cases of fratriphagy were noticed amongst aged specimens, but as no animosity had been apparent beforehand, it was possibly due to a temporary protein deficiency in the diet. The staples of the diet adopted were mixed grain and hard fruits, with an occasional ration of nuts, honey and fat bacon; this proved acceptable and adequate for the maintainance of all normal activity, including reproduction and the rearing of young. Water was always provided in the cages, and in hot weather was frequently drunk, though in the natural habitat it can seldom be available.

The feeding habits of the animal in the wild have not yet been determined by observation; most of the specimens handled had been kept alive for some days pending transit, during which time they were necessarily fed upon an artificial diet, so that a study of stomach contents could disclose nothing, and in the few examples that were taken dead the material contained no recognisable fragments. It may safely be inferred, however, that it is normally granminivorous and frugivorous rather than phytophagous. In trapping, it was noticed that under stress of deprivation it readily lapses into carnivority, partially eaten specimens having several times been found with the living in pitfalls which had not been promptly emptied, and this trait was later confirmed in captivity, as mentioned above. The small vegetation of its habitat is rich in species which fruit and seed freely, such as *Casuarina pusilla*, *Brachyloma ericoides*, *Lepidosperma laterale*, *Kunzea pomifera* and *Triodia* spp., and there is no doubt that these provide the mainstay of its diet.

The animal is rapidly debilitated by high temperatures, and most of the deaths sustained in the captive series occurred during heat waves in mid-summer.

In the wild, several ectoparasites occur, the chief of which is a *Laelaps;* this is very difficult to eradicate in captivity, though it may be kept in check by frequent dusting with pyrethrum; in moderate numbers it apparently works no detriment to the hosts. The animal has no characteristic smell.

Reproduction and Development

Of the entire series of 69 examined, 33 are males, 33 females and three undetermined; fully adults totalled 20, and in the remainder, subadults of medium growth predominate markedly over earlier stages and nestlings; the latter having been obtained by excavation of burrows and by breeding in captivity. The pitfall method of trapping chiefly adopted precludes an adequate representation of the more immature stages, since these are not independently active at night, and is unable, therefore, to indicate accurately the prevalence of reproduction at any one time. Incidentally, it is noteworthy that of adults taken in pitfalls, females are three times as numerous as males.

Sufficient evidence has been obtained, however, to show that the main natural breeding season falls in autumn and early winter. The earliest new-born litters

observed were in the third week of May, but advanced nestlings have been found in June also, and knowledge of the life cycle subsequently obtained indicates that these must have been produced as early as the beginning of May, with mating therefore in April. On the other hand, some young collected in November, must by the same argument have been littered as late as mid-August. The apparent absence of a natural breeding season in summer depends largely upon negative evidence, all activities of the species being much more obscure in the hot weather. However, the batches trapped in October and November contained no pregnant females, and of the many females kept in captivity only one became pregnant during the hot months. In captivity, males have been observed attempting intercourse as early as the tenth week, but all pregnant females observed, both in the wild and in captivity, have been fully adult.

In the number of embryos produced there is considerable variation, from four to seven having been observed in *utero;* in the latter case five occupied the right and two the left horn; superior development of the right horn has been observed also in recently evacuated uteri in which the number of young was unknown. Litters of as few as three and as many as six thriving nestlings have been taken, but the normal complement seems to be four, as with most Pseudomyds. Whether a single female may produce more than one litter in a season has not been ascertained.

Testis enlargement in the male is restricted to a very short period, probably only from March to April. Of 20 adult or advanced subadult males trapped between May and November only one showed any scrotal prominence, and this was a subadult. An interesting feature in the series of males reared in captivity is the markedly superior gonad development of subadult as compared with fully adult males. In the wild this has already been noted in some Central Australian species.

Three litters of young have been successfully reared in captivity; two of these were born in captivity of females pregnant when taken, while the third was removed from a nest when about three weeks old. Two of the mothers with normal-sized litters were assiduous in their attentions to the nestlings and, although very gentle and permitting themselves to be touched and handled without resentment, became much agitated when the young were removed. The third, with six young, was overtaxed and apparently unable to nourish them all adequately, and within a few days ejected two young from the nest. They were found stiff and cold on the cage floor, but when restored to the nest quickly recovered, only to be thrown out again the next night; they struggled on for seven days under this nightly rejection before succumbing, and in general all nestlings observed have shown great vitality. They adhere very firmly to the nipples of the dam, and when startled into leaving the nest hurriedly she frequently dragged them with her over the cage, but not as a routine matter as recorded for *Conilurus*, etc.

The females occasionally made a shrill chirruping bird-like call, and the young a more feeble squeak, but both young and parents were less vocal than some other local murids similarly kept and observed.

For the first three months the nestlings were weighed and examined weekly, and the following condensed summary gives the main facts of their development so observed; the weights quoted are averaged for the members of the three litters:

At three days—Weight 3 grammes; eyes shut; dorsum haired nearly black; belly nearly nude, pink and with sharp demarkation from dorsum.

At two weeks—5·5 grammes; coat close, coarse and very dark; belly fur developing fast; white to base.

At three weeks—7·0 grammes; head and body 50 mm; tail 38; pes 14·5; manus 6·5, ear 6; eyes open; dorsal fur 9 mm. long, still dark and shaggy; belly completely furred with the middle areas now dark-based; ears closely adpressed to head; tail sparsely furred but already sparsely sprinkled with dark brown dorsally.

At four weeks—9·0 grammes; dorsal fur more erect and the pale subterminal band just appearing.

At five weeks—10·0 grammes; dorsal coat erect and fluffy and showing much of the basal slate colour and the pale subterminal band.

At six weeks—13 grammes; time of weaning was not observed but the young were now much abroad both day and night, and eating grain and other hard foods.

At seven weeks—14 grammes; moult begun.

From eight to fourteen weeks—Weights were: 14·5, 16, 16, 16·5, 17, 17, 19 grammes, respectively.

At fifteen weeks—Moult completed; most of the young were now heavier than the parents, but still retained many signs of immaturity, especially in the head and body length and in the ear, which was decidedly smaller, and in the thin fluffy ungrizzled coat.

At twenty-three weeks (one example)—Head and body 77 mm.; tail, 80; pes 19·5; ear 15.

In the development of these nestlings an anomaly was met with in the marked precocity of one example, which at an early stage was left (by a series of accidents) the sole survivor of the original litter. At the fifteenth week this example weighed 22·5 grammes, and at the eighteenth week had head and body 76 mm., pes 20, ear 16, outstripping in linear dimensions the young of full litters by five weeks. The point is of some interest as affording a possible clue to the causation of at least part of the apparently capricious variation in dimensions so frequent in several Australian rats.

The growth changes were not followed up into adult life, but it seems unlikely that the mean adult dimensions in nature could be attained in less than nine months, and twelve months is more likely. Evidence derived from the duration of captivity (which has exceeded two years in some cases) and the maturity of such examples when taken, suggests a specific life-span of about four years.

External Characters

The series examined consists of 69 specimens, of which a large proportion have been examined in the flesh before preservation. Twenty are fully adult, and the rest form a developmental series which bridges the gap to the naked nestling stage. Of the total, 25 have been kept under observation in captivity for periods up to 30 months. There is little evidence of change in structural characters having been effected in this way, but for reasons of orthodoxy the statements which follow on the external characters of the species are drawn entirely from the strictly feral material.

Bodily size small to medium, the head and body length averaging 85 mm. and reaching 93 mm., and the live weight about 16 grammes. Build moderate; appendages slender and long. The relative head size is much as in such forms as *Ps.* (*Leggadina*) *hermannsburgensis;* the ratio, head and body length: skull length, about 1 : 30, as in that species, but the fur contour has an enlarging effect. The fur profile of the head is convex with a prominent erect tuft in the anterior nasal region, due to an opposition ridge just behind the rhinarium. The eye rather prominent with a diameter from canthus to canthus of 3·5 mm., approxi-

mately; well fringed with black lashes. Mysticial vibrissae very strongly developed; the longest bristles about 35 mm.; the anterior members white, the posterior black, and the intermediate (and longest) black with white tips. The supraorbitals, 22 mm. long, and entirely black; genals weak or lacking. The ear very large; length to 18 mm.; breadth across the trough of pinna to 9 mm. The development of the ear exceeds that of the eremian *minnie* and approaches that of the less specialised species of *Notomys;* its length is about 20% of the head and body length. The substance of the ear is thin and membranous, and pale except at the extreme margin, where slight epidermal darkening takes place; in life it is a delicate pink, as are all exposed areas of epidermis.

Manus, length to 8·5 mm., breadth transversely across palm from base of second digit to 3·5 mm. and third digit 3 mm.; rather slender in general proportions, but (as is frequently the case) appearing stouter in many subadults in which the palmar structures are plumper and broader than in calloused adults. The palm pale pink and unpigmented; its central area markedly granular, the granularity extending to the basal portion of the underside of the digits, where the transverse ridges are broken into rows of granules and are not continuous as is usual. The grooving of the digits is deep and prominent, averaging eight upon the third digit. Claws rather stout, their free projection about equal to the apical pads; moderately fringed, but the hairs not quite reaching the claw tip. Ulnar carpal vibrissae large—reaching 7 mm. Palmar pads of moderate size and development; conspicuous more from the granularity of the surrounding areas than by their own relief, which is but moderate in adults; the outlines of the pads are well defined anteriorly but are sometimes indefinite posteriorly, where the relief is much lower. In a few subadults the pads are very strongly developed, with their anterior portions lifted free of the palm, and their margins somewhat angular, as in *Leporillus*. All pads smooth or very faintly striate.

The detailed shape and relative development of the pads is subject to much variation. The carpals are always much larger (though variably so) than the interdigitals and are relatively narrow. The outer is longer than the inner, and most frequently has at least twice its area; the inner has a well-marked accessory fold adjoining the pollux. The first [2] interdigital is usually round, but may be subtriangular or bell-shaped; the second or median interdigital is rather constantly pyriform, and the third which is shaped (and varies) like the first, has usually either a small satellite at its postero-external corner, or a low heel formed by the conjunction of two smaller satellites; quite frequently, however, both these accessories are absent. In point of relative size, there is a marked tendency for the median interdigital to be dominant and the laterals subequal; when the laterals depart from subequality, $3 > 1$ more often than $1 > 3$. Subequality of all three interdigitals is rare, but is more frequent in subadults than adults.

Variation of all the pads, both carpals and interdigitals, is to a large extent truly individual, and most of the variants may be found in nestlings of 17 days' growth. While these differenees are confusing when a few examples only are compared, systematic examination of the whole series leaves no doubt that the arrangement most characteristic of the species is: outer carpal > inner carpal > second interdigital > third interdigital = first interdigital.

Pes—Length to 22·5 mm., breadth transversely across the sole from the base of first digit, to 3·5 mm., and the third digit to 5 mm. General form decidedly long and slender, the length averaging 25% of the head and body and the

[2] In these papers the pad which is actually and functionally the first interdigital on the pollical side of the palm, is so numbered in descriptions and formulae, but it is probably homologous with the second interdigital of the primitive pentadactyle manus.

length ÷ breadth ratio, ca. 7·0. The width of the sole maintained posteriorly, not tapering markedly to heel which does not project conspicuously beyond the malleoli. The posterior plantar surface is nearly smooth or with the usual transverse crease lines, but the interdigital portion is characteristically verrucose, as in the manus. The undersurface of the digits well grooved, the third digit carrying ten grooves and the ridges basally broken into rows of granules as in the manus. In some nestlings the undersurface of the digits and the interdigital basin carry scattered hairs. Nails stout; their projection and fringing as in the manus.

Pads of moderate size and prominence; more distinctly striate than in the manus and remarkably constant in general shape and proportion, and thereby in sharp contrast to the manus. The inner metatarsal, narrow and much elongated but with its posterior termination low and vague; it is commonly three to four times the length of the outer metatarsal which is small and rounded or oval; in two examples only is there a departure from this condition, and in these the metatarsals are subequal. The first interdigital large and bell-shaped, the second broadly pyriform or oval and usually differing conspicuously from the third which is smaller and of narrower shape, and the fourth broadly oval or bell-shaped, rarely with a conjoined satellite, and usually subequal or slightly larger than interdigital one.

The pad formula therefore is: Fourth interdigital = first interdigital > second interdigital > third interdigital > inner metatarsal (in area) > outer metatarsal.

The *tail* is almost always longer than the head and body, averaging 118% in adults and 114% in subadults; there are, however, one or two cases of subequality in the feral series, and in the captive series tails shorter than the head and body are not uncommon; there is a suspicion, however, that such cases are due to mutilations which have healed without obvious defect. The tail is slender and evenly tapering and capable of considerable flexure in life. The tip is well covered with the steadily lengthening tail hairs which exceed it by 3 mm.; there is no exposed calloused knob. Scale counts are rather variable, averaging middorsally ca. 19 per centimetre.

Testes relatively small and never greatly swollen; scrotum lightly furred white, and its epidermis unpigmented.

Mammae—Posterior 9 mm. from clitoris; anterior 9 mm. from posterior.

The *vulva* is usually completely occluded in virgin females, and a similar condition may develop in adult females after parturition, if they are denied access of the male. In two cases observed in captivity, it was found that 21 weeks after the birth of litters which were reared in the absence of the male parent, the vulva was almost completely sealed externally by what appeared to be a considerable tissue connection between the labiae.

PELAGE

The original description, which was founded on 14 living or just dead examples holds good with little modification for the whole series, but the additional material permits of some amplification of the first account.

In the limited area from which specimens have been so far obtained the species proves to be one of very constant pelage. Sexual and seasonal variation is scarcely demonstrable, age variations are only marked at early growth stages, and such differences as do occur, therefore, may be regarded as of individual origin and varying incidence of the moult. About 5% of the series are slightly warmer and less glaucus in tone than the type series described; in the coldest blue-grey examples, the colour of the subterminal zone of the fur is near Ridgway's "Tilleul Buff" and the tips of the guard hairs are cold black, resulting in a general

dorsal colour near "Mouse Grey"; in the warmer coloured coats the subterminal zone is near "Vinaceous Buff" and the guard hairs terminate in brownish-black.

The ventral fur at base is normally plumbeous throughout, but in one or two examples white-based fur occurs on gulo-sternal and abdominal areas. The ear, when furred grey-brown as described originally, is moderately well contrasted with the dorsal coat; sometimes, however, the ear back is haired with a grizzle of near black and silver, and is then less so. There is in a large proportion of examples a supra calcaneal darkening (formerly overlooked) caused by a grizzling of the white hairs of the lower leg with black or blackish-brown; the effect is usually slight, however, and never forms a prominent marking. The darkening of the dorsum of the tail is very variable; in a few examples it is sufficiently marked to attain a fairly sharp contrast with the whitish sides and lower surface, but usually takes the form of a sparse grizzling of blackish hairs along a narrow dorsal strip extending from two-thirds to three-quarters of its length; the pencilling ceases very abruptly and the terminal one-third to one-quarter is pure white on all surfaces. While the darkest tails are all of adult or aged examples, white tails are less characteristic of immaturity than was thought, and most examples of half-growth show a noticeable pencilling of the dorsum.

The rearing of three litters in captivity enabled the following facts on the early development of the pelage to be ascertained. Within three days of birth the dorsum (which is already pigmented a deep slate) is sparsely haired with black or near black, while the non-pigmented ventrum is pink and hairless and with sharp demarcation. At two weeks the dorsal fur is dense enough to obscure the skin and is close and coarse, while the belly fur which is entirely white is much thinner, though developing fast. At three weeks the dorsal coat is 9 mm. long and shaggy, the first lifting from the prone adpressed condition having begun and the belly fur darkening at the base over the central parts of the area. Even at this early stage (head and body 50 mm.) the coat is already bipilous, though the long black contour hairs are much more numerous than the second pile. At four weeks the second pile is much better developed and has a distinct though dull ashy middle zone, a brownish tip and a short plumbeous basal zone. This condition leads on by increase in amount and length of the second pile and increase in the proportion of the basal blue zone, to the fluffy, erect, blue appearing pelage characteristic of immaturity up to about the head and body 70 mm. stage. This immature pelage is very similar in composition to that of adults, but is sparser, finer and more erect and therefore with a greater exposure of the basal leaden zone; its guard hairs are fewer and both piles are spun out to very attenuated tips, which in the main pile are more frequently brown than in adults, while on flanks and rump a sprinkling of white tips occurs.

The first *moult* begins at about the seventh or eighth week and may not be completed until the fifteenth; spreading downward from the nape its progress can be readily followed by the pale line of demarcation caused by the more prominent ashy subterminal zone of the new coat, as well as by its greater density and grizzling.

In the wild, the adult pelage is evidently subject to heavy attrition, which has the effect of breaking off the points of the black guard hairs and of thinning out the main pile, so that ultimately, in adults, a partial return to the glaucus immature condition is effected. This is made good by a second annual moult, which is well illustrated by one adult example in captivity (in November), in which the entire dorsal epidermis is obscured by a dense carpet of the emerging ashy renewal coat. Although this is the only example actually observed at the change, study of the entire feral series shows that worn and thin pelages are to be found

together with rich recently renewed ones on the same dates both in winter and summer, justifying the inference that the time of moult is governed by individual rather than seasonal factors.[3]

In captivity, quite marked changes are induced in the pelage even in one life cycle. At five weeks captive litters are conspicuously darker and longer furred than wild born ones at the same stage, and both distinctions are retained and accentuated as growth continues. Six advanced subadults at the head and body 78 mm. stage show much richer pelage than in any feral examples; the over-all length of the coat (15 mm.) is about the same, but the proportion of guard hairs reaching this length is greater and the main pile is 2 mm. longer and the general density higher. Further, the basal plumbeous and terminal zones are darker and the subterminal zone is more strongly contrasted and richer coloured.

Immersion in 80% alcohol for ten years has produced marked changes in colouration in all but a few of the series so preserved, and a large proportion of these would scarcely be suspected of specific identity with field skins; in particular, the characteristic glaucus tone of the natural pelage disappears very rapidly.

Flesh Dimensions (feral specimens only)

The following figures give, in millimetres, the range and mean values for the dimensions of (1) a group of adults selected as free from any obvious immaturity in external characters, (2) a group of subadults of decidedly inferior bulk, (3) a long-furred independent nestling, (4) a short-furred nestling of approximately 17 days' growth.

	1		2		3	4
	3 ♂	6 ♀	11 ♂	9 ♀	♂	♀
Head and body	86–80 (84)	93–80 (87)	76–70 (71·5)	78–65 (68·5)	50	45
Tail	108–97 (101)	113–90 (99·5)	96–72 (82)	90–70 (78·5)	70	36
Pes: length	22·5–21 (21·5)	22·5–20 (21·0)	21–18·5 (19·5)	20–18·5 (19·5)	18	13
Pes: breadth	—	3·5–3·0 (3·1)	3·5–3·0 (3·3)	3·5–3·0 (3·1)	—	2·8
Manus: length	—	8·0–8·0 (8·0)	8·5–8·0 (8·2)	8·0–7·5 (7·7)	7·5	6·0
Manus: breadth	—	3·5–3·0 (3·3)	3·0–2·8 (2·9)	3·0–2·8 (2·9)	2·8	2·8
Ear: length	18·5–16 (17)	18–16 (17)	17–15 (15·5)	17–13·5 (15)	14	6
Rhinarium to eye	13–13 (13)	14–11 (12)	12–10 (11)	11·5–9 (10·0)	—	7
Eye to ear	12–10 (11)	11–9 (10)	11–8·5 (9)	10–8 (9·0)	—	6
Weight (in grms.)	16–12·5 (13·8)	18·5–18 (18)	9–8 (8·5)	8–7 (7·5)	—	—

The dimensions quoted for the species in the original description are well within the range of the adult group, but slightly below the mean values and decidedly below the maxima as now ascertained. The general level of variation in these selected groups of adults and subadults is actually higher in most items than in the eremian *hermannsburgensis;* but the individual and capricious variation involving major anomalies in development as shown by the concurrence of maxima and minima in the same example, such as occurs in several series of Central Australian rats recently reviewed, is absent. Here the occurrence of maxima for pes, ear and tail is always associated with a high head and body value and high body weight, and conversely immaturity can nearly always be detected by low values for ear and tail. The earsize is an especially useful first criterion of immaturity; even advanced subadults may usually be readily recognised by the smaller area of the pinna.

[3] I have demonstrated a similar state of things in the rock wallaby, *Petrogale penicillata herberti.* Trans. Roy. Soc. S. Aust., **55,** (1931), 84

Sexual differentiation in dimensions is very slight and, in adults, of doubtful significance; examination of the subadult series, however, seems to suggest that at some intermediate stages the male develops more rapidly than the female; but the data is insufficient to establish this.

The extraordinarily rapid development of appendages at the fourth or fifth week of life, while the head and body length remains almost constant, is well shown by a comparison of the two nestlings; in the more advanced (4), at the stage of early erect pelage, when the head and body length is still only 59% of the adult average, the pes is already 86%, the ear 82%, and the tail 70%, of their final values.

The effect of captivity upon the linear dimensions of wild born examples is slight, the only demonstrable change being a failure to attain the normal mean ear length of feral examples; young reared entirely in captivity may, as already indicated, attain much greater body weight, but whether their ultimate linear measurements are similarly increased is uncertain, no captive born example having yet reached complete maturity.

Skull Characters

A series of 22 skulls has been examined, all removed from animals of known external characters, dimensions and history; half of them are derived from animals kept in captivity for varying periods, but as with external characters, the following account is based on the feral series alone.

The salient features of the skull in a general view, are its lengthened nasal region, over-all narrowness, and very fragile zygomata. The ossification is light. The general dorsal aspect is fairly constant throughout the series, but there are one or two examples in which an arrested development of the anterior root of the zygoma accentuates the leptoprosopic character, and one such anomaly (the only fully adult example available at the time) was responsible in the original description for the phrase "very peculiar" as applied to its shape; this is now seen to be somewhat over-stated for the series as a whole. Immature skulls, with shortened facial region, are quite similar in general dorsal appearance to the more bulbous forms of *hermannsburgensis*.

Muzzle region as originally given; the point contact with the frontals is variably developed, but usually the termini take the form of characteristic prongs, distinctly separated and penetrating the labyrinth of the fronto-nasal suture. The width of the nasals increases fairly evenly towards a distal maximum, with a slight constriction at the beginning of the terminal third. The maxillary fossae are unusually well developed in old skulls, and the opening of the bursa is conspicuous dorsally. The anteorbital fossa rather large in adults much smaller in immature skulls—the external wall bent strongly inwards. The zygomatic outline varies considerably; in the majority the anterior width is not markedly less than the posterior, and the outline tends to parallelism or even slight concavity, with smooth angles both before and behind; in others, however, the arches are more prominently thrown out from the skull and decidedly wider posteriorly. In the interorbital constriction variation in width is largely individual and not strongly influenced by age; the supraorbital edges, however, show the customary bevelling with advancing development. Lacrymals narrow; their free margin often irregular. Braincase of the suddenly expanded type, and fairly constant in development and shape. Interparietal of moderate size; not spanning the braincase, and its shape crudely rectangular rather than subtriangular and with its interior margin often irregular.

In lateral view, the upper profile is low and little arched and the occiput smoothly rounded, without angularity at the lambda. The margin of the zygo-

matic plate slopes forwards as stated, but the angle of slope varies considerably, in general being steeper in adults than in young skulls; the condition under all three of these heads very similar to what may be seen in *waitei*, *hermannsburgensis* and *patrius*. The posterior palate is conspicuously wide and flat; the anterior palatine foramina also large, both long and widely open, tapering towards the incisors and in adults with the maximum width nearly always posterior to the midpoint; posteriorly the foramina always reach beyond the anterior margin of M^1 and sometimes reach the lingual cusp of the first lamina. The mesopterygoid fossa large and wide open; in adults the walls are parallel or nearly so, but in young skulls the maximum width is at the palatal margin. The parapterygoid variable; in fully adults the fossa is distinctly developed with a sunken floor and raised ectopterygoid margin (as in the original description); in others (usually subadult) the floor is flat and much less enclosed; the fenestration of the floor of the parapterygoid fossa is remarkably variable also. Bulla decidedly small for the size of the skull and little inflated; its age change, as described under *hermannsburgensis*.

Dentition weak; upper incisors variably ophisthodont; upper molar rows straight and nearly parallel; gradation in size from M^1-M^3 moderate, as in *Pseudomys* s. str.

General structure of molar crowns much as in *Notomys*, the buccal cusp of the first lamina of M^1 obsolete and much reduced on the others. Contrary to the original description, the posterior displacement of the lingual cusp of the first lamina of M^1, is now seen with more suitable material, to be considerable and the obliquity of this lamina is equal to that of *hermannsburgensis* and *patrius* of the group *Leggadina*. There are no supplementary cusps on either upper or lower molars. Mandible weak. Sexual variation inappreciable.

Skull Dimensions

The following figures give, in millimetres, the skull dimensions of (1) four adult males all showing appreciable wear on the first lamina of M^1, and extracted from animals free from any immaturity in external characters, (2) three adult females in the same age group, (3) one subadult female of head and body length 70 mm.

	1	2	3
Greatest length	26·8–25·5 (25·9) ;	26·8–25·0 (26·0) ;	23·2
Basal length	22·1–20·6 (21·4) ;	22·4–20·0 (20·8) ;	18·5
Greatest Zygomatic breadth	12·3–11·8 (12·1) ;	12·4–11·7 (12·1) ;	11·4
Braincase: breadth	11·7–11·5 (11·6) ;	12·1–11·4 (11·7) ;	11·2
Interorbital breadth	4·0–3·7 (3·9) ;	4·0–3·7 (3·9) ;	3·9
Nasals: length	10·0–9·0 (9·5) ;	10·5–8·8 (9·7) ;	8·2
Nasals: greatest breadth	2·5–2·3 (2·5) ;	2·5–2·4 (2·4) ;	2·1
Palatal length	13·7–13·0 (13·3) ;	13·9–12·6 (13·3) ;	11·7
Palatilar length	12·2–11·9 (12·1) ;	12·5–11·0 (11·7) ;	10·3
Ant. Palatine Foramina length	6·0–5·0 (5·5) ;	5·9–5·0 (5·4) ;	5·0
Ant. Palatine Foramina breadth	1·7–1·5 (1·6) ;	1·8–1·7 (1·8) ;	1·4
Bullae: length	3·7–3·5 (3·6) ;	3·7–3·5 (3·6) ;	3·2
Upper molars	3·9–3·6 (3·7) ;	3·9–3·6 (3·8) ;	3·9

In the feral series the agreement in dimensions between examples of the same basal length is close, and these, in turn, are roughly proportional to body size, the variation in this latter group being about 5% in the case of the head and body: skull length, ratio. In the captive series, although little or no structural change can be detected, anomalies in both the above groups of metrical relationships are

more marked. Molar wear in both moieties of the series is variable, and if unsupported by other evidence is unsatisfactory as a criterion of age.

RELATIONSHIPS

Material for direct and detailed comparison with *glaucus* and *albocinereus* (apparently the nearest allies of the present species) is still lacking, so that the recorded dimensions remain the chief criteria by which the identities of the three species may be judged. The slight modification to the original figures for *apodemoides*, necessitated by examination of the new series, does not appreciably alter the previous assessment of its position.

The flesh dimensions of *glaucus* may now be completely merged in those of *apodemoides*, but the figures for the skull of the former are all higher except that of the anterior palatine foramina, which is slightly below the mean for *apodemoides*.

With respect to *albocinereus* of Western Australia, the effect of the new data is to close the gap metrically between *apodemoides* and the typical *albocinereus*, so that the South Australian animal is intermediate between the two described varieties of the latter. A large anterior palatine foramen seems characteristic of *apodemoides;* both the maximum length (6·0) and the mean (5·4), exceeding that of the decidedly larger *albocinereus typicus* skull.

EXPLANATION OF PLATES XII TO XV

PLATE XII

A typical habitat of *Pseudomys* (*Gyomys*) *apodemoides;* a general westerly view from a ridge near the eastern boundary of the Hundred of Coombe, South Australia.

PLATE XIII

Three views of adult examples of *Pseudomys* (*Gyomys*) *apodemoides*, in captivity. (x 0·75 ca.) (The tail shortening in the upper example is traumatic.)

PLATE XIV

A, B, C, Dorsal aspects of the skull of *Pseudomys* (*Gyomys*) *apodemoides*, as shown by an immature ♂ example of head and body length 67 mm., by an average adult ♂, and by a very aged ♂, respectively, and illustrating the progressive age changes in the cranial and facial regions. (x 2·8, 2·6, 2·4.) D, Palatal aspect of the skull of the average adult ♂ figured at B. (x 2·6.) E, Lateral aspect of the same. (x 2·6.)

PLATE XV

A, B, free margin of the zygomatic plate in an immature ♂ example of head and body length 67 mm., and in an aged ♀, respectively, showing age changes in this feature. (x 9·0 ca.). C, Unworn upper molars of the right side in an aged ♀ (x 9·0 ca.). D, Worn upper molars of the right side in an aged ♀ (x 9·0 ca.) E, Worn upper molars of the right side in a similarly aged example of *Pseudomys* (*Leggadina*) *patrius* Thomas and Dollman. (x 9·0 ca.) for comparison of the obliquity of the laminae with C and D. (The supplementary cingular cusp has been deleted.) F, Right pes of an adult ♀ (x 3·3 ca.) G, Right manus of an adult ♀ (x 4·0 ca.), weak type. H, Ditto of another adult ♀ (x 4·0 ca.), stout type.